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Myrmica lonae Finzi, 1926 – a species separate from *Myrmica sabuleti* Meinert, 1861 (Hymenoptera:Formicidae)

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Abstract

Morphological and ecological evidence for the separate species identity of *Myrmica lonae* Finzi 1926 and *M. sabuleti* Meinert 1861 is presented. The female castes of *M. lonae* differ from *M. sabuleti* in particular by the larger width of basal scape lobe and the smaller maximum distance of frontal lobes. All individual gynes and about 97 % of the worker nest samples can be separated by a discriminant function using these characters. The habitat segregation of *M. lonae* and *M. sabuleti* is very strong. The main habitat of *M. lonae* is xerothermous woodland (56 % of samples), followed by open peat bog (20 %), and open xerothermous habitats (19 %). Only 11 % of the *M. sabuleti* nests were found in xerothermous woodland, 83 % in open xerothermous habitats, and no nest was found in peat bogs. Both habitat selection and geographic distribution indicate *M. lonae* to be the less thermophilic species; in Fennoscandia, it stretches 200 – 300 km farther north and it seems to be absent from the Mediterranean south of 40° N where *M. sabuleti* is still abundant.

Within the sympatric range, syntopic occurence was noted in 19 % of the geographic sites. The data do not suggest increased hybridisation in case of syntopic occurrence and doubtful samples are better considered as a result of intraspecific variation rather than representing hybrids. The *M. lonae* populations from peat bogs have a significantly enlarged scape lobe compared to conspecific populations from other habitats.

Zusammenfassung

Myrmica lonae Finzi 1926 – eine von _Myrmica sabuleti_ Meinert 1861 verschiedene Art

Morphologische und ökologische Argumente für die Heterospezifität von *Myrmica lonae* Finzi 1926 und *Myrmica sabuleti* Meinert 1861 werden dargestellt. In den weiblichen Kasten unterscheidet sich *M. lonae* von *M. sabuleti* insbesondere durch die grössere Weite des Scapuslobus und den geringeren Maximalabstand der Frontallappen. Alle Gynen und 97 % der Nestproben der Arbeiter können mittels Diskriminanzfunktionen, die diese beiden Merkmale verrechnen, unterschieden werden. Die Habitatwahl von *M. lonae* und *M. sabuleti* ist sehr unterschiedlich. Das Vorzugshabitat von *M. lonae* ist xerothermes Waldland (56 % der Proben), gefolgt von offenen Torfmooren (20 %) und offenen xerothermen Habitaten (19 %). Dagegen wurden nur 11 % der Nester von *M. sabuleti* in xerothermen Waldland, 83 % in offenen xerothermen Habitaten und kein Nest in Torfmooren gefunden. Sowohl Habitatwahl als auch geographische Verbreitung weisen *M. lonae* als die weniger thermophile Art aus; in Fennoskandien geht sie 200 – 300 km weiter nach

Norden und sie scheint im Mediterranen Raum südlich von 40° N nicht mehr vorzukommen, während *M. sabuleti* hier noch häufig ist. Innerhalb des sympatrischen Gebietes beider Arten wurde ein syntopes Vorkommen für 19 % der Fundorte festgestellt. Die morphologischen Daten liefern keine Hinweise für erhöhte Hybridisierungsfrequenzen an Orten mit syntopen Vorkommen. Zweifelhafte Proben sind daher besser durch intraspezifische Variation als durch stattgefundene Hybridisierungen zu erklären, obwohl letztere nicht auszuschließen ist. Die *M. lonae* Populationen aus Torfmooren haben im Vergleich zu konspezifischen Populationen aus anderen Habitaten einen signifikant grösseren Scapuslobus.

1. Introduction

After much confusion in the first half of the 20th century, the interpretation of the myrmicine ant species *Myrmica sabuleti* Meinert 1861 has remained stable beginning from Sadil up to the present. ARNOLDI (1970), COLLINGWOOD (1979), KUTTER (1977), SADIL (1952) and SEIFERT (1988, 1996) obviously named the same species as *M. sabuleti*. It seems that no revising previous author has ever seen a type specimen of Meinert and such material was also not available for the present author. An interpretation of *M. sabuleti* is thus only based on Meinert's original desription that states for the male a scape as long as one-third of the funiculus, the legs with long erect hairs, and a petiole strongly rugose. The worker is described as having an almost rectangularly bowed scape base with a dent and dorsal longitudinal carina and ear-shaped frontal lobes. 10 of the 12 *Myrmica* species possibly occuring in the terra typica do not show such a combination of male and worker characters. As possible candidates for this name remain only *M. sabuleti* in the present understanding and *M. lonae* Finzi. However, Meinert did not mention the presence of a very big or massive scape lobe and *M. lonae* is definitely rarer in this region than *M. sabuleti*. Hence, there is much hope that the present definition of *M. sabuleti* will remain stable in case of discovery of genuine type material.

Myrmica sabuleti has a W Palaearctic distribution and reaches W Siberia just in N Kazakhstan. SEIFERT (1988) has synonymised two taxa with *Myrmica sabuleti*: *Myrmica scabrinodis* subsp. *lonae* Finzi 1926 and *Myrmica sabuleti* var. *spinosior* Santschi 1931. Recently, however, he treated *M. lonae* as bona species in his guide on Central European ants (SEIFERT 1996). The most obvious morphological difference of *M. lonae* is the much larger scape lobe (compare Figs. A102 and A117 in SEIFERT 1996 ; Figs. Ja, Jb, La, and Lb in KLEIN et al. 1998). However, the considerable variation of scape lobe size within both *M. lonae* and *M. sabuleti* complicates the separation of both entities and raises some doubt on their heterospecifity. This paper presents morphological and ecological arguments that a separate treatment of *M. lonae* is an acceptable decision and gives information on polymorphism within the *M. sabuleti* species complex in Europe.

2. Material studied

284 worker samples with 929 specimens and 80 queen samples with 111 specimens from altogether 183 geographic sites were morphometrically investigated. They came from the following regions: the British Isles (6 samples), Fennoscandia and Denmark (78), France and the Benelux countries (10), Central Europe (208), the Balkans and Asia Minor (16), Spain (26), and Italy (8). The worker samples were to 98 % nest samples and in 2 % of the cases local samples (random hand samples or contents of the same pitfall trap).

The material included the following type specimens:

Types of *Myrmica sabuleti* ssp. ***lonae*** Finzi 1926, stored in the Museum of Comparative Zoology of the Harvard University Cambridge Massachusetts/USA: 1 worker lectotype (by present designation) from Karislojo (Finland), leg. Forsius; 3 worker paratypes from Monte Baldo (Trentino/Italy), 1923.07; 3 worker paratypes from Monte Manos (NE of Triest, now in Slovenia), leg. Finzi 1923.05; 1 worker and 1 gyne paratype from Ratzes/Tirol (=Razzes/Trentino).

The type worker of *Myrmica sabuleti* var. ***spinosior*** Santschi 1931 labelled '*Pyren.occ. Irun. 25 – 26.3.1926 Lindberg, M.sabuleti v. spinosior Typus*', Naturhistorisches Museum Basel.

3. Methods and terminology

Morphometry

Measurements were made on mounted and dried specimens using a goniometer-type pin-holding device, permitting endless rotations around X, Y, and Z axes. A Technival 2 (Zeiss Jena) or a M10 (Wild) stereo microscope was used at magnifications of 100 – 225x. The maximum possible magnification to keep a structure within the range of the ocular micrometer was used. A mean measuring error of 2 µm was calculated for smaller structures such as FR, but one of ± 4 µm for larger structures such as gyne mesosoma length. To avoid rounding errors, all measurements were recorded in µm even for characters for which a precision of ± 1 µm is impossible. 10 morphometric characters were investigated:

CL – maximum cephalic length in median line; the head must be carefully tilted to the position with the true maximum. Excavations of occiput and/or clypeus reduce CL.

CW – maximum cephalic width; in *Myrmica* always across eyes

FL – maximum distance of the frontal lobes

FR – minimum distance between frontal carinae

ML – mesosoma length in the alates; measured in lateral view from the caudalmost portion of propodeum to the frontalmost point of the anterior pronotal slope (i.e. not to the frontalmost point of the whole pronotum that is usually concealed by the occiput!).

PEW – maximum width of petiole

PPW – maximum width of postpetiole

SL – maximum straight line scape length excluding the articular condyle

SP – maximum length of propodeal spines. Arithmetic mean of both spines measured in dorsofrontal view from spine tip to the bottom of the meniscus formed between the spines. This mode of measuring is less ambiguous than other methods but results in some spine length in species with reduced spines.

SW – maximum distance between caudal lobe margin and anterior scape margin measured perpendicular to the longitudinal scape axis. The scape must be carefully tilted untill the maximum distance is situated in the measuring plane. This is given in dorsofrontal position as defined by SEIFERT (1988, 1996).

Habitat typing

Only the spots from which nest samples have been collected were used for habitat typing. Four main habitat categories were distinguished, using information provided by plant species composition, plant coverage, inclination, and geologic outcrop:

(1) open xerothermous: xerothermous and semi-dry grasslands or open xerothermous heath (usually with *Calluna*)

(2) open mesophilic: mainly mesophilic grasslands with higher grasses

(3) open moist to wet: sunny peat bogs

(4) thermophilic woodland: sunny woodland with *Pinus*, *Quercus*, or *Castanea* as main tree species

If not otherwise stated, statistic tests tested the equality of mean values: a **t** test was applied, when an **F** test proved the equality of the variances; otherwise a modified **t** test with corrected degrees of freedom according to WELCH (1947) was applied.

4. Results

4.1 The morphological distinctness of *Myrmica sabuleti* and *M. lonae*

Based upon worker nest sample means and individual gynes, two distinct clusters can be demonstrated within the W Palaearctic *M. sabuleti* complex (Tabs. 1 and 2, Fig. 1).

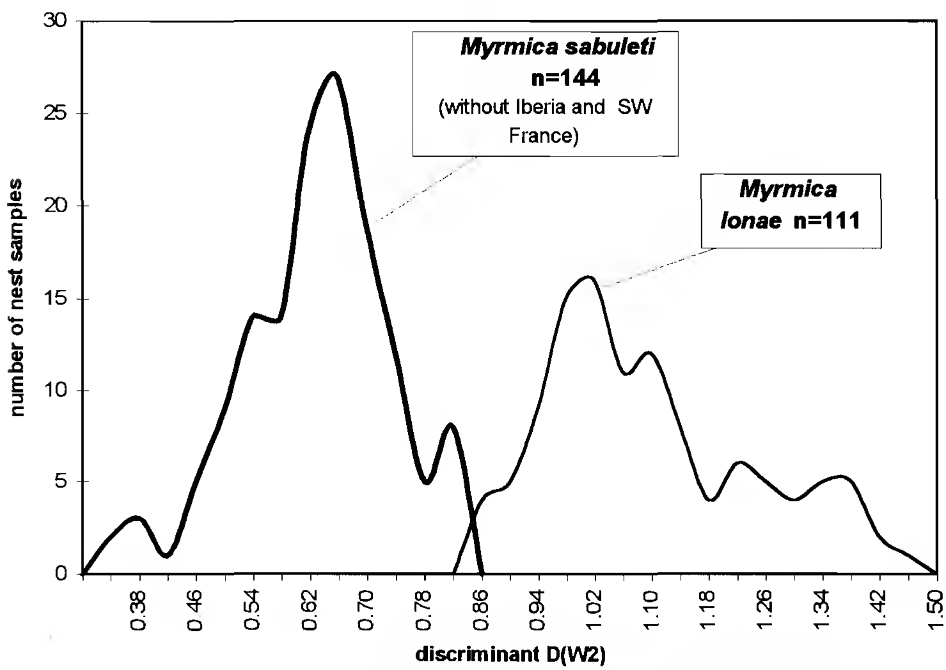

Fig. 1 Discriminant D(W2) of worker nest sample means of *Myrmica lonae* and *M. sabuleti* with D(W2)– 6.5 SW/SL – 0.30 CW/FL.

Tab. 1 Morphometric data of workers of the European *Myrmica sabuleti* species complex. D(W2) is a linear discriminant with D(W2) = 6.5 SW/SL – 0.30C W/FL. Note that the number of measured individuals is only 52, 63, and 56 for *M. lonae*, *M. sabuleti*, and SW Mediterranean *M. sabuleti* respectively in case of the characters CL/CW, PEW/CW, PPW/CW, and SP/CL.

☿☿	individuals			nest sample means		
	M. lonae	***M. sabuleti***	***M. sabuleti*** SW Mediterranean	***M. lonae***	***M. sabuleti***	***M. sabuleti*** SW Mediterranean
	(n=385)	(n=467)	(n=77)	(n=111)	(n=144)	(n=29)
CW	1178 ± 63 [980, 1389]	1146 ± 64 [930, 1313]	1168 ± 80 [967, 1365]	1183 ± 52 [1057, 1329]	1145 ± 49 [1016, 1253]	1175 ± 74 [1010, 1333]
SW/SL	0.260 ± 0.024 [0.206, 0.329]	0.197 ± 0.019 [0.146, 0.267]	0.157 ± 0.016 [0.132, 0.205]	0.263 ± 0.021 [0.227, 0.316]	0.196 ± 0.016 [0.151, 0.228]	0.158 ± 0.014 [0.137, 0.200]
CW/FL	2.046 ± 0.068 [1.831, 2.268]	2.155 ± 0.066 [1.956, 2.390]	2.238 ± 0.066 [2.087, 2.382]	2.041 ± 0.057 [1.892, 2.195]	2.159 ± 0.049 [2.032, 2.306]	2.241 ± 0.059 [2.116, 2.352]
FL/FR	1.644 ± 0.098 [1.399, 1.931]	1.525 ± 0.078 [1.299, 1.722]	1.344 ± 0.067 [1.228, 1.488]	1.648 ± 0.084 [1.461, 1.885]	1.522 ± 0.063 [1.370, 1.669]	1.338 ± 0.068 [1.234, 1.451]
CW/FR	3.359 ± 0.171 [2.864, 4.001]	3.284 ± 0.150 [2.756, 3.765]	3.006 ± 0.139 [2.776, 3.397]	3.361 ± 0.138 [3.005, 3.856]	3.285 ± 0.114 [2.982, 3.652]	2.996 ± 0.120 [2.778, 3.184]
SL/CW	0.814 ± 0.020 [0.748, 0.889]	0.812 ± 0.020 [0.759, 0.870]	0.838 ± 0.022 [0.786, 0.897]	0.814 ± 0.016 [0.767, 0.852]	0.811 ± 0.016 [0.772, 0.855]	0.837 ± 0.019 [0.801, 0.882]
SP/CL	0.392 ± 0.021 [0.348, 0.434]	0.399 ± 0.024 [0.334, 0.457]	0.375 ± 0.022 [0.329, 0.429]			
CL/CW	1.025 ± 0.020 [0.976, 1.060]	1.027 ± 0.017 [0.983, 1.061]	1.031 ± 0.017 [0.991, 1.062]			
PEW/CW	0.284 ± 0.015 [0.257, 0.325]	0.285 ± 0.014 [0.256, 0.333]	0.280 ± 0.014 [0.254, 0.322]			
PPW/CW	0.405 ± 0.014 [0.380, 0.455]	0.407 ± 0.018 [0.376, 0.468]	0.402 ± 0.014 [0.350, 0.431]			
D(W2)	1.078 ± 0.167 [0.719, 1.542]	0.632 ± 0.128 [0.272, 1.105]		1.097 ± 0.148 [0.843, 1.474]	0.625 ± 0.108 [0.307, 0.836]	

The *Myrmica lonae* cluster has a much larger SW/SL, a notably smaller CW/FL, and slightly larger CW/FR in both castes than the *M. sabuleti* cluster. No differences were found in scape length, width of waist segments, spine length, and head length indices. There are significantly positive allometries of SW/SL for both *M. sabuleti* and *M. lonae* the consideration of which, however, does not change determinations. A discriminant function

$$D(W2) = 6.5\ SW/SL - 0.30\ CW/FL$$

in the workers and

$$D(G2) = 7.839\ SW/SL - 0.512\ CW/FL$$

in the gynes offers a sufficiently good separation of both entities. As *Myrmica sabuleti* were interpreted worker nest samples with D(W2) < 0.84 and as *M. lonae* such with D(W2) >0.84. About 7 samples, or 2.8 % of the total, which were found in the interval D(W2) [0.81, 0.87], are of uncertain determination. All individual type specimens of *M. lonae* are 'typical': D(W2) is 1.250 in the lectotype of *M. lonae* from Karislojo, 0.963 – 1.022 in four paratypes from M. Baldo, 1.096 – 1.232 in three paratypes from M. Nanos, and 1.192 in the paratype from Ratzes. Gynes have a D(G2) < 0.73 in *M. sabuleti* and > 0.75 in *M. lonae*. The paratype gyne of *M. lonae* from Ratzes has D(G2) of 1.137.

The SW Mediterranean population of *M. sabuleti* (found in Iberia and SW France) significantly differs from the *M. sabuleti* population of the remaining territories by less diverging frontal lobes, a very small scape lobe, and a longer scape (Tabs. 1 and 2). However, discriminant functions using nest sample means as the operational unit did not provide a convincing separation of this population that does not deserve a taxonomic name.

Tab. 2 Morphometric data of gynes of the European *M. sabuleti* species complex. D(W2) is a linear discriminant with D(G2) = 7.839 SW/SL - 0.512 CW/FL

	M. lonae (n=45)	***M. sabuleti*** (n=60)	***M. sabuleti*** SW Mediterranean (n=6)
CL	1320 ± 40	1322 ± 32	1307 ± 80
	[1184, 1386]	[1249, 1384]	[1215, 1414]
CW	1325 ± 40	1334 ± 37	1317 ± 94
	[1226, 1383]	[1242, 1412]	[1198, 1402]
ML	2004 ± 71	2029 ± 72	2008 ± 125
	[1869, 2114]	[1879, 2190]	[1843, 2123]
SW/SL	0.268 ± 0.021	0.203 ± 0.014	0.171 ± 0.030
	[0.233, 0.326]	[0.173, 0.231]	[0.141, 0.205]
CW/FL	2.078 ± 0.053	2.217 ± 0.080	2.247 ± 0.122
	[1.976, 2.178]	[2.070, 2.402]	[2.139, 2.437]
CW/FR	3.134 ± 0.151	3.163 ± 0.156	2.902 ± 0.114
	[2.833, 3.555]	[2.877, 3.615]	[2.700, 3.014]
FL/FR	1.508 ± 0.075	1.428 ± 0.071	1.294 ± 0.070
	[1.382, 1.687]	[1.319, 1.641]	[1.231, 1.399]
SL/CW	0.764 ± 0.016	0.749 ± 0.017	0.801 ± 0.045
	[0.736, 0.793]	[0.713, 0.786]	[0.733, 0.862]
D(G2)	1.035 ± 0.173	0.458 ± 0.123	
	[0.756, 1.511]	[0.161, 0.726]	

4.2 Habitat selection and geographic distribution of *M. sabuleti* and *M. lonae*

In 98 nest samples of *M. lonae* and 107 of *M. sabuleti* the habitat was known. The data show clearly different patterns of habitat selection and provide further arguments for a heterospecifity of *M. lonae* and *M. sabuleti*. 83.2 % of the *M. sabuleti* nests were found in open xerothermous habitats, only 11.2 % in xerothermous woods, and no nest was found in open boggy habitats. Hence, *M. sabuleti* is distributed over the main habitat types as is typical for a thermophilic ant species. The habitat selection of *M. lonae*, however, deviates strikingly: as much as 56.1 % of the *M. lonae* nests were found in xerothermous woods, 20.4 % in open boggy places, and 19.4 % in open xerothermous habitats. Each of these ratios is significantly different between both species for $p < 0.0001$ if tested in the X^2 test. Open mesophilic habitats, in the study area these are usually meadows with higher grasses, normally do not provide optimum climatic conditions for brood development and are inhabited by both *M. sabuleti* and *M. lonae* in equally small frequencies (5.6 % vs. 4.1 %).

Tab. 3 Distribution of the nest samples of *Myrmica lonae* and *M. sabuleti* over four main habitat categories.

Habitat category	*Myrmica lonae* (n=98)	*Myrmica sabuleti* (n=107)
(1) open xerothermous	19 (19.4 %)	89 (83.2 %)
(2) open mesophilic	4 (4.1 %)	6 (5.6 %)
(3) open boggy	20 (20.4 %)	0 (0 %)
(4) xerothermous wood	55 (56.1 %)	12 (11.2 %)

The peculiar habitat selection of *M. lonae* deserves a more detailed consideration. Undoubtedly *M. lonae* is a rather thermophilic but to a lesser degree than *M. sabuleti*. In xerothermous grasslands of Central Europe it is usually replaced by *M. sabuleti* and other thermophilic *Myrmica* species. However, occurrence on open xerothermous grasslands as a subdominant ant with estimated densities of 5 – 15 nests/100 m^2 is no real exception. Such populations were found by the author near Poxdorf and near Wittersroda in Thüringen/Germany or near Sierre in Valais/Switzerland. As a rule, such xerothermous grassland populations do occur in Central Europe in localities with closely-neighboured source populations of *M. lonae* in xerothermous woodland. In S Finland, were the main competitors *M. sabuleti* or *M. specioides* are absent or extremely rare, *M. lonae* is a dominant *Myrmica* on S-exposed xerothermous grasslands on sand or gravel.

A peculiarity of *M. lonae* is its occurence in open parts of peat bogs. Such populations were found in S Sweden near Röke (leg. Douwes) and near Krokstrand (leg. Collingwood) and in the Netherlands near Lichtenvoorde (leg. Elmes). In Germany, *M. lonae* is a typical ant of the peat bogs of the northern foothills of the Alps, where it was found in the Harprechtsmoos near Eisenharz (leg. Seifert), the Gründlenried near Ravensburg (leg. Klingseis), a bog near Benediktbeuern (leg. Seifert), a bog near Wallgau (leg. Douwes), and in the Schönramer Filz near Teisendorf (leg. P. Hartmann). The populations in the peat bogs near Eisenharz and near Benediktbeuern both showed densities of 7.5 nests/100 m^2.

M. lonae was here a subdominant ant species and avoided the wettest parts of the habitat.

Xerothermous woodland is the most important habitat for *M. lonae* in Central Europe, the southern slopes of the Alps, and the Balkans. Main tree species are either *Pinus silvestris*, *Quercus petraea*, *Quercus robur*, *Quercus pubescens*, *Pinus nigra*, or *Castanea sativa* depending upon phytogeography. Geological outcrop and tree species composition, however, are of no direct importance for *Myrmica lonae*. The necessary condition for brood development in Central Europe is merely a sufficient amount of sun-exposed spots on forest floors. On the southern slopes of the Alps, *M. lonae* is obviously a typical ant in xerothermous forests between 450 and 1100 m.

The habitat selection indicates *Myrmica lonae* to be less xerothermophilic than *M. sabuleti*. This picture is confirmed by geographic distribution. *M. lonae* goes north to 61° N in Scandinavia and to 62° 30' in Finland. *M. sabuleti* reaches 58° 40 N in Scotland and S Scandinavia and seems to be entirely absent from Finland. The southernmost known sites of *M. lonae* in the Balkans and Asia Minor are situated at 41° N while *M. sabuleti* goes south to 37° N in Greece and the Iberian peninsula. *M. lonae* is so far not known from the southern British Isles, the entire Iberian peninsula, SW France and the Apennines. Within the whole study area *M. lonae* is much less abundant than *M. sabuleti* and is known from 59 sites:

AUSTRIA: Ferlach – 7 km SW, 1994.07.11; Rifenal – 1.5 km N, 1997.06.20; Roppen – 1 km E, 1994.07.04; BULGARIA: Dobrostan, 1982.09.10; FINLAND: Finström: Bergö, 1987.07.28; Karislojo (leg. Forsius); Lahti – 21 km E, 1996.07.11; Nauvo, Seili, 1984.08.03; Savonlinna, 1961.06; GERMANY: Baden-Württemberg: Eisenharz – 2 km SE, 1993; Ravensburg: Gründlenried, 1992; Bayern: Wallgau, 1986.08.20; Benediktbeuern – 5 km WSW, 1994.07.06; Garmisch-Partenkirchen – 12 km W, 1994.08.23; Teisendorf – 6NE, Schönramer Filz; Hessen: Breitenbach, 1978.05.31; Erda – 1 km NW, 1999; Nordrhein-Westfalen: Lengerich 1 km E, 1999.05.08; Niedersachsen: Lingen – 4 km NW, 1995; Lingen – 7 km NW, 1995.09.06; Sachsen: Niederoderwitz, 1920.09.12; Lichtentanne, 1993.07.18; Rochsburg – 0.5 km S, 1993.06.21; Scharfenstein – 2 km S, 1993.06.22; Tharandt – 1.5 km E, 1993.05.15; Tharandt - 0.9 km E, 1998.06.19; Weesensteine near Pirna, 1962.06.12; Zwickau-Auerbach – 1 km SE, 1979.09.01; Chemnitz, 1915; Sachsen-Anhalt: Quenstedt, 1980.06.07; Thüringen: Berkach, Grüne, 1996.09.05; Seebergen near Gotha, 1996.06; Poxdorfer Hang, 1986; Wittersroda – 1 km W, 1993.07.20; Schleswig-Holstein: Leck – 3 km S, Langenberger Forst, 1997; ITALY: Trentino: M. Baldo, 1923.07; Bozen – 23 km E, Ratzes; Meransen, 1992.06.17; Triest-NE: M.Nanos, 1923.05; KROATIA: Mrkviste, 1910.06.27; THE NETHERLANDS: Lichtenvoorde; NORWAY: Halden, 1958; SCOTLAND: Loch Maree; SWEDEN: Gotland: Helvi, St. Olofsholm, 1978.08.17; Bohus Län: Krokstrand, Stromstad; Skåne: Röke, Fäljemyrs, 1979.05.26; Östergotten: Geta, 1977.08.05; Vist, 1958.04.24; Öland: Borgholm, 1992.06.14; Byrums Sandvik, 1992.06.14; Träby, 1992.06.12; SWITZERLAND: Gordola, Sassone, 1997.06.10; Locarno, Mte Brè, 1997.05.13; Messen, Schürmatt, 1997.05.15; Pfynwald, Sierre 1990.07.14; Saverne (Forel); TURKEY: İlgas; İnebolu – 20 km S, 1989.07.10; Kastamonu – 40 km N, 1990.05.20.

4.3. Syntopic occurrence and hybridisation

Among the sites situated in geographic regions with sympatric ranges of *M. lonae* and *M. sabuleti*, a minimum of 2 samples with an average of 4.5 samples per site was available from 53 sites. Syntopic occurrence was observed in 10 of these sites.

Predicting the number of sites with syntopic occurrence for the assumption of a random distribution needs an estimation of the overall abundance ratio of *M. sabuleti* vs. *M. lonae* in the considered territories. A ratio of 0.57 : 0.43, as suggested by the material evaluated morphologically, is fully misleading since there was a strong sampling bias for sites with *M. lonae*. Faunistic and ecological investigations performed by the author in the years 1978 – 2000 outside and within the presented research project resulted in an estimated overall abundance ratio of *M. sabuleti* vs. *M. lonae* of 8 : 1. Under this assumption, 23 out of 53 sites are predicted to provide samples of both species in simulations with homogeneously distributed random numbers and a homogeneous variation between 2,3 ... 7 samples per site. Predicted and real values are significantly different for $p < 0.01$ in an X^2 test, which indicates a trend for interspecific spatial exclusion. Since sampling was not restricted to a single habitat type in many study sites, the strong habitat segregation is possibly not the full explanation for this trend.

Hybridisations should reduce the distance of D(W2) from the indifference value 0.84, here expressed by the equation DIST = ABS [D(W2) – 0.84], and increase the coefficients of variation in D(W2), here expressed by the equation cVAR = SD/D(W2). However, 47 nest samples from sites with both species did not show decreased distances and increased intranidal variation compared to 201 samples from sites with only one species (Tab. 4), which indicates that hybrid frequencies are not increased in case of syntopic occurrence. Occasional proximity to the indifference value is thus better explained by intraspecific variability rather than being the result of hybridisations. It is difficult to decide from the morphological data if hybridisation really occurs. It seems possible in 7 samples with large variation in size of scape the lobe. Three such samples were found on Öland Island/SE Sweden.

Tab. 4 Data of worker nest samples of *Myrmica lonae* and *M. sabuleti*. DIST = distance of the nest sample means of D(W2) from the indifference point 0.84. cVAR = intranidal coefficient of variation of D(W2).

	nest samples from sites with both species (n=47)	nest samples from sites with only one species (n=201)
DIST	0.2513 ± 0.1771 [0.0159, 0.6342]	0.2252 ± 0.1118 [0.0031, 0.5437]
cVAR	0.0711 ± 0.0496 [0.0071, 0.2163]	0.0808 ± 0.0494 [0.0016, 0.2472]

4.4. Influence of nest habitat on morphology

The possible influence of the nest habitat on the expression of discriminative characters might be questioned. In fact, this influence is very weak in both species (Tab. 5). The only exception is that bog populations of *M. lonae* have increased SW/SL and decreased CW/FL. These differences are significant for $p < 0.0001$ if compared with the populations from xerothermous woodland.

Several explanations of this difference seem possible. It remains to be investigated if there is an adaptive value of heavily sclerotised structures at *Myrmica* scape bases. If reflecting a genetic difference, scape lobe enlargement in bog *M. lonae* is more likely a pleiotropic effect of a selection for an unknown physiological adaption. Modificatory epigenetic effects of differing temperature and humidity conditions on character expression seem also possible.

Tab. 5 Expression of some morphological characters of *Myrmica sabuleti* and *M. lonae* depending upon habitat type in worker nest sample means.

Habitat type		***Myrmica lonae***		***Myrmica sabuleti***	
Open xerothermous	CW	1171 ± 46	(n=19)	1145 ± 51	(n=89)
	SW/SL	0.265 ± 0.023	(n=19)	0.198 ± 0.013	(n=89)
	CW/FR	2.027 ± 0.062	(n=19)	2.151 ± 0.050	(n=89)
Open bog	CW	1191 ± 57	(n=20)	no data	
	SW/SL	0.282 ± 0.021	(n=20)	no data	
	CW/FR	1.996 ± 0.032	(n=20)	no data	
xerothermous wood	CW	1175 ± 52	(n=55)	1160 ± 32	(n=12)
	SW/SL	0.255 ± 0.016	(n=55)	0.202 ± 0.014	(n=12)
	CW/FR	2.064 ± 0.053	(n=55)	2.169 ± 0.046	(n=12)

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